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RESPONSES OF MAMMALIAN INSECTIVORES, AMPHIBIANS, AND REPTILES TO BROAD-SCALE MANIPULATION OF COARSE WOODY DEBRIS
(AGREEMENT NO. SRS 00-CA-11330138-197)

Final Project Report
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EXECUTIVE SUMMARY

There is mounting evidence that course woody debris (CWD) is an important habitat component for small terrestrial animals, particularly shrews and salamanders (e.g., Butts and McComb 2000). Few studies of these animals, however, have separated the influence of CWD from the influences of other habitat components. Arguably, this can only be accomplished with the large-scale manipulation of CWD. Further, few studies have examined the importance of CWD outside of coniferous forests of the Pacific Northwest.

The USDA Forest Service at the Savannah River National Environmental Research Park established a template of 9.3-ha plots in 1997 for the purpose of better understanding the role of dead wood in southeastern pine ecosystems (McCay et al. in press). The template was established within managed, loblolly pine (*Pinus taeda*) forests on the Upper Coastal Plain Physiographic Province. This ecosystem differs strongly from those that have been well studied in the Pacific Northwest. This report describes our study of the population responses of shrews, amphibians, and reptiles to the large-scale manipulation of CWD within that environment. In particular, we compared capture rates and demographic parameters of shrew, amphibian, and reptile populations at sites from which fallen dead wood was removed ("all removal" and "down removal" plots combined) and sites from which dead wood was not removed ("control" and "catastrophic" plots combined).

Early in the project, we realized that these relatively xeric forests are habitat for many species that typically inhabit moist environments, such as star-nosed moles (McCay et al. 1999), shrews (1)[1] and many types of amphibians (2,3). The movement of these species, however, seems greatly associated with precipitation. For example, star-nosed moles (*Condylura cristata*) in this environment apparently disperse through upland pine habitats during intense rain events (McCay et al. 1999). The capture rates

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[1] Numbers refer to sections of this report.

of shrews are strongly correlated with rainfall after seasonal and long-term time trends have been accounted for (McCay in prep). Rainfall and the creation of temporary ponds are of great importance to amphibian migration and breeding in this environment (3). In times with low precipitation, CWD may be of increased importance to forest-floor animals because of its ability to absorb environmental moisture (Jaeger 1980).

The shrew response to removal of CWD was apparently negative, but subtle compared to natural population fluctuations over time (1). We found strong evidence, however, that populations of *Cryptotis parva* declined following removal of dead wood (P = 0.02). We also found some evidence (P = 0.07) of population decline for *Blarina carolinensis*. Age structure of *B. carolinensis* populations during winter suggested (P = 0.06) that there were more mature individuals and fewer young individuals at removal plots than control plots. Thus, immigration of individuals from more productive areas might be mitigating the negative influence of CWD-removal on population size of *Blarina* (Van Horne 1983; Pulliam 1988). Among the three species of shrews present at the study site, *Cryptotis* may have been most sensitive to CWD removal because its density across the landscape is low. Thus, its ability to immigrate to "sink" habitats might be low.

We captured 20 species of amphibians at CWD-monitoring plots, including 6 species of salamanders and 14 species of frogs and toads. There were no significant declines in abundance of salamanders, individually (P > 0.05) or as a group (P = 0.34), at removal plots. Although anurans as a group did not differ in abundance between control and removal plots (P = 0.25), *Pseudacris crucifer* was more commonly captured at removal than control plots (P = 0.04). No other anuran species varied with removal of dead wood. Thus, we failed to see a strong effect of CWD removal on amphibians. Because most of these species are wetland breeders, it is possible that patterns of migration to or from wetlands may have confounded our comparisons (3). However, abundances of two non-wetland breeders at our plots were also not affected by removal of dead wood (*Plethodon glutinosis*, P = 0.84; *Pseudotriton ruber*, P = 0.19).

We captured 29 species of reptiles at our plots, including 9 species of lizards and 20 species of snakes. Many species were captured incidentally, some represented by only a single capture (2). Interestingly, 6 of 9 species of lizards had greater capture rates at removal plots than control plots. However, capture rates of lizards, did not differ as a group (P = 0.14) or individually (P > 0.05). Capture rates of snakes did not differ as a group (P = 0.66) or individually (P > 0.05) according to removal treatment.

In sum, we found weak responses by most forest-floor vertebrates to the removal of CWD. This weak response, however, should not be taken as evidence that dead wood is an unimportant habitat component for these species. The forests of the study area are characterized by low ambient levels of dead wood (McMinn and Hardt 1994). There may exist a response threshold below which populations respond only subtly to changes in dead wood abundance. If so, manipulations that involve additions of dead wood, rather than removals, might evince greater faunal responses. Loeb (1999) found that the addition of dead wood to pine forests of the study area led to drastic increases in the abundance of cotton mice (*Peromyscus gossypinus*). We are encouraged that Castleberry and Ford (Personal Communication) are using additions of dead wood to explore faunal responses at these study sites.

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Pulliam HR. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

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ADDITIONAL PRODUCTS

In addition to the papers presented herein, the following presentations and papers emanated (or will emanate) from work completed under this agreement.

Presentations

McCay TS, Hanula JL, Loeb SC, Lohr SM, McMinn JW, and Wright-Miley BD. 1999. The role of coarse woody debris in southeastern pine forests: Preliminary results from a large-scale experiment. Symposium on the Ecology & Management of Dead Wood in Western Forests, Reno, Nevada, November. Oral presentation.

McCay TS and Komoroski MJ. 2001. Response of shrews to experimental removal of dead wood in a southeastern pine forest. 81st Annual Meeting of the American Society of Mammalogists, Missoula, Montana, June. Oral presentation.

McCay TS. 2002. (Planned) Population dynamics of shrews in a warm-temperate environment. International Colloquium: Biology of the Soricidae II, Rector, Pennsylvania, October. Oral presentation.

Publications

McCay TS, Hanula JL, Loeb SC, Lohr SM, McMinn JW, and Wright-Miley BD. In Press. The role of coarse woody debris in southeastern pine forests: Preliminary results from a large-scale experiment. Proceedings of the Symposium on the Ecology & Management of Dead Wood in Western Forests. PSW-XXX. USDA Forest Service, Pacific Southwest Research Station, General Technical Report.

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RUNNING HEAD: Shrew response to removal of dead wood

DEMOGRAPHIC RESPONSES OF SHREWS (MAMMALIA: SORICIDAE) TO EXPERIMENTAL REMOVAL OF DEAD WOOD

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ABSTRACT.—We sampled shrews at 9.3-ha plots from which logs ≥ 10 cm diameter were manually removed (n = 6) and control plots (n = 6) in loblolly pine (*Pinus taeda*) forests of the southeastern coastal plain. Samples were taken seasonally between autumn 1997 and summer 2001. Capture rates of *Cryptotis parva* were lower at plots from which dead wood was removed (P = 0.024); whereas, capture rates of *Blarina carolinensis* (P = 0.066) and *Sorex longirostris* (P = 0.353) did not differ between control and removal plots. There was some evidence that age distribution of *Blarina* at removal plots was skewed toward older individuals during winter (P = 0.06), suggesting that removal plots may have acted as population sinks in the landscape. *Cryptotis* may have been most sensitive to the removal of CWD because of low population density and, therefore, poor ability to move into areas of low reproduction. Effect of CWD removal on population dynamics of these shrews was relatively subtle compared to strong seasonal and multi-year trends in abundance.

Key words: *Blarina*, coarse woody debris, *Cryptotis*, managed forests, population dynamics, *Sorex*

The abundance of coarse woody debris (CWD) has been positively associated with population size of certain shrews in the Pacific Northwest (Butts and McComb 2000, Carey and Johnson 1995, Lee 1995). *Sorex trowbridgii* and *S. monticolus* were captured more frequently in old growth forests, with abundant CWD, than regenerated forests, with little CWD, on the Olympic Peninsula (Carey and Johnson 1995). Capture rates of *S. trowbridgii* were positively associated with abundance of dead wood at 7 regenerated forests (Carey and Johnson 1995). Similarly, capture rates of *S. trowbridgii* were positively associated with cover of logs at both stand and microhabitat spatial scales in Douglas fir forests of western Oregon (Butts and McComb 1995).

Few studies of shrews have attempted to separate the influence of CWD from the influence of other environmental factors, such as density of vegetation. Lee (1995) studied shrews in Douglas-fir forests from which CWD was removed according to management prescription. Contrary to expectations, *S. vagrans* was captured more frequently on 1-ha plots from which dead wood was removed (Lee, 1995). *Sorex monticolus* and *S. trowbridgii* were not captured more frequently at control plots than plots from which CWD was removed; however, both of these species demonstrated greater reproductive activity at control plots (Lee 1995). Thus, demographic responses to the removal of CWD may not be limited to changes in abundance.

Environmental moisture strongly influences the abundance and distribution of many shrews (Getz, 1961). Coniferous forests of the Pacific Northwest are characterized by high environmental moisture and high abundance of dead wood (Harmon et al. 1986). Because dead wood has the ability to retain moisture (Harmon et al. 1986, Jaeger 1980), abundance of CWD may be more important to shrews in relatively dry habitats, such as pine forests on well-drained soils in southeastern North America. Furthermore, pine forests of the Southeast generally have lower natural abundances of dead wood (McMinn and Hardt 1996) and lower heterogeneity in vegetation than coniferous forests of the Pacific Northwest. The role of CWD in pine forests of the Southeast is, thus, unclear (McMinn and Crossley 1996).

The nature of the use of dead wood by shrews also is not clearly known. Most authors have suggested that dead wood benefits shrews by providing food resources, protection from predators, or appropriate den and nest sites (see Loeb 1996 for review). Importance of these factors may vary with the shrew species. On the southeastern coastal plain of North America, southern short-tailed shrews (*Blarina carolinensis*) are relatively fossorial and largely rely on subterranean invertebrates (McCay 2001). Southeastern shrews (*Sorex longirostris*) and least shrews (*Cryptotis parva*) are epigeal and largely consume arthropods at the litter layer (Whitaker and Hamilton 1998). The fossorial *B. carolinensis* might be less dependent on CWD at the forest floor than epigeal shrews with which it is syntopic.

We studied shrews at plots subjected to experimental removal of CWD to better understand the importance of dead wood to shrews in pine forests of the southeastern United States. Large, replicated plots and extensive sampling over time allowed us to rigorously examine the role of dead wood in population dynamics of these species.

METHODS

Study site.—The study was conducted at the Savannah River National Environmental Research Park in the upper portion of the Coastal Plain Physiological Province, South Carolina USA (33º0-25'N, 81º25-50'W). Climate of the region was warm temperate, with hot summers and cool, mild winters.

This study was part of a larger effort to better understand the ecological role of dead wood in managed southeastern pine forests (McCay et al., *in press*). The study was designed as a randomized complete block with four treatments replicated in three blocks. Blocks were forest stands chosen subject to the following criteria: forested with approximately 45-year-old loblolly pine (*Pinus taeda*) plantations; ≥ 76 m from nearest wetland, road, and power line; and able to accommodate four square 9.3-ha plots. Each plot consisted of a 6-ha core area, surrounded by a 3.3-ha buffer area subject to the same treatment as the core area (Fig. 1). Buffer areas were not used for surveys to avoid edge effects. Timber harvesting was prohibited within 61 m of plots. All plots were thinned to achieve a standing basal area of 13.8 - 20.8 m^2 ha^{-1} and intentionally burned on a uniform rotation.

Within each stand, each of the four plots was randomly assigned to one of the following treatments: removal of all snags and fallen logs, removal of fallen logs only, felling and girdling to simulate a catastrophic input of dead wood, and control. Snags and fallen logs considered in this study were ≥ 10 cm diameter at the large end and ≥ 60 cm long. A private crew under USDA Forest Service supervision removed dead wood in summer 1996 and each winter 1997-2000. The catastrophic input of dead wood was implemented following completion of the present study; thus, catastrophic plots were considered additional controls. Because the removal of snags should have little effect on populations of shrews, which reside exclusively at the forest floor, we considered both removal treatments together.

Field Sampling.—We sampled shrews using a series of pitfall-drift-fence arrays (Fig. 1). Aluminum flashing was used as drift fencing, and 19-l plastic buckets were used as pitfall traps. At each plot, we installed a single, centrally located X-shaped array (Campbell and Christman 1982) with 30-m arms. Between the central array and each corner of the plot we installed a Y-shaped array (Kirkland and Sheppard 1994) with 15-m arms. Traps were opened during a 14-day period in each of winter (January), summer (July), and autumn (October), and during a 28-day period in spring (March). Traps were kept dry and supplied with a small amount of soil and other forest debris. Traps were checked daily between 0600-1200 h; large distances among plots and the remote nature of the study area precluded more frequent checking of traps. Shrews were identified, weighed, and uniquely marked using toe clips. Shrews that died during trapping were removed to the laboratory for necropsy.

Necropsy.—Shrews were weighed to the nearest 0.1 g in the lab after drying and cleaning of the pelage. Sex was determined by gross examination of the internal organs. Age was estimated using relative tooth wear. For each species, a 12-class aging system (ranging 1- to 4+) was devised based on Pearson (1945) for *B. carolinensis* and Rudd (1955) for *S. longirostris* and *C. parva*. For analyses presented here, classes were combined (for example, 2-, 2, and 2+ were combined to 2), resulting in four age classes (ranging 1 to 4) to increase sample sizes. All specimens have been accessioned into the zoological collections of the Georgia Museum of Natural History or Colgate University.

Data Analysis.—Capture rates were represented as unique captures per plot-day. Strong seasonal trends in capture rates prompted us to remove them as a confounding factor in analyses. Seasonal effects were estimated for each plot and removed from the data following the procedure of Kendall (1976) for additive seasonal effects. Effect of CWD removal on residuals was analyzed using repeated-measures analysis-of-variance (Milliken and Johnson 1992). Significance of temporally autocorrelated factors was evaluated using the procedure of Greenhouse and Geiser (1959). Data were blocked by forest stand.

Influence of wood removal on shrew weight was examined using analysis-of-variance. Shrew weight was blocked by age and sex because of the strong influence of these factors on animal size. Factors affecting age distributions were analyzed using log-likelihood-ratio tests. Because of small sample sizes for summer and autumn, age distributions were compared only for winter and spring.

RESULTS

Abundance.--We captured 285 unique *B. carolinensis* individuals. Capture rate of *Blarina* exhibited a strong seasonal trend, with an annual peak during spring and an annual low during summer-autumn (Fig. 2). Capture rates of *B. carolinensis* at control plots did not differ from capture rates at removal plots (Treatment: $F_{1,8} = 4.53$; $P = 0.066$). Capture rate declined during the four-year sample period (Time: $F_{3.1,8} = 18.61$, $P < 0.001$), but declined similarly at control and removal plots (Time × Treatment: $F_{3.1,8} = 1.95$, $P = 0.146$). We captured 164 unique *S. longirostris* individuals. Capture rate of *Sorex* exhibited a moderate seasonal trend, with greatest capture rates in spring (Fig. 2). Capture rates of *S. longirostris* at control plots did not differ from capture rates at removal plots (Treatment: $F_{1,8} = 0.97$; $P = 0.353$). Capture rate declined strongly during the four-year sample period (Time: $F_{2.2,8} = 20.42$, $P < 0.001$), but declined similarly at control and removal plots (Time × Treatment: $F_{2.2,8} = 1.00$, $P = 0.395$). We captured 73 unique *C. parva* individuals. Capture rate of *Cryptotis* exhibited a weak seasonal trend (Fig. 2). Capture rates of *C. parva* at control plots were greater than capture rates at removal plots (Treatment: $F_{1,8} = 7.75$; $P = 0.024$). Capture rate did not change over the four-year sample period (Time: $F_{3.7,8} = 2.07$, $P = 0.114$).

Population Structure.--Weights of *B. carolinensis* did not differ by removal treatment when sex and age were accounted for ($F_{1,31} = 0.45$, $P = 0.5038$; Table 1). Age distributions of *Blarina* during spring were similar at control and removal plots ($G^2 = 1.12$, $P = 0.77$, df = 3; Fig. 3). There was some evidence that age distributions of *Blarina* differed between control and treatment plots during winter ($G^2 = 7.29$, $P = 0.06$, df = 3), with a greater proportion of individuals in the youngest age class at control plots. Weights of *C. parva* did not differ by removal treatment when sex and age were considered ($F_{1,31}$ = 0.43, P = 0.5175; Table 2). Age distributions of *Cryptotis* were similar at control and removal plots during spring (G^2 = 2.71, P = 0.26, df = 2) and winter (G^2 = 0.22, P = 0.64, df = 2; Fig. 4). Weights of *S. longirostris* did not differ by removal treatment when sex and age were accounted for ($F_{1,89}$ = 0.04, P = 0.8470; Table 3). Age distributions of *Sorex* were similar at control and removal plots during spring (G^2 = 5.22, P = 0.16, df = 3) and winter (G^2 = 1.06, P = 0.78, df = 3; Fig. 5).

DISCUSSION

The importance of dead wood to shrews has been long presumed, but rarely examined. We provide evidence that the removal of large pieces of dead wood from southeastern pine forests can reduce the ability of forests to support shrews. Like Carey and Johnson (1995) and Lee (1995), however, we found that the importance of dead wood varies among shrew species. Among the three shrews on the southeastern coastal plain, *Cryptotis parva* was the most sensitive to the removal of CWD. The low apparent size of the population may have made *C. parva* particularly sensitive to changes in its environment. *Blarina carolinensis*, the most commonly captured species in our assemblage, also showed some evidence that removal of dead wood affected its population dynamics.

There was subtle evidence that populations of *Blarina* at removal plots were skewed toward older individuals during the breeding season. This is consistent with the notion that these areas were acting as population sinks in the landscape (Pulliam 1988, Van Horne 1983), receiving immigrants from areas of greater reproduction outside of the plot. Direct evidence of reproduction among captured shrews did not provide the data necessary to rigorously examine this hypothesis.

Our experiment was limited to the effect of relatively large (≥10 cm) pieces of dead wood. Shrews may use this resource at a finer spatial scale than we were able to detect. Smaller pieces of dead wood may serve an important role in the population dynamics of these species and mitigate the influence of CWD removal. We encourage studies into the relative importance of dead wood of various sizes at various spatial scales.

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Table 1. Mean (± SD) weight of *Blarina carolinensis* captured at plots from which dead wood was removed (Removal) and left intact (Control). Shrews were aged using relative tooth wear. Sample sizes are given in parentheses.

		Treatment	
Sex	Age	Control	Removal
Male	1	6.62 ± 0.92 (38)	6.34 ± 0.74 (19)
	2	6.61 ± 1.30 (9)	6.50 ± 0.81 (7)
	3	8.80 ± 1.34 (11)	9.24 ± 0.89 (9)
	4	9.28 ± 1.23 (5)	9.51 ± 1.30 (7)
Female	1	6.68 ± 1.01 (21)	6.22 ± 0.70 (9)
	2	6.71 ± 1.32 (7)	6.75 ± 1.51 (6)
	3	8.33 ± 1.77 (6)	8.17 ± 0.15 (3)
	4	– (0)	8.83 ± 1.16 (4)

Table 2. Mean (± SD) weight of *Cryptotis parva* captured at plots from which dead wood was removed (Removal) and left intact (Control). Shrews were aged using relative tooth wear. Sample sizes are given in parentheses.

		Treatment	
Sex	Age	Control	Removal
Male	1	3.6 ± 0.8 (10)	3.3 (1)
	2	4.0 ± 0.5 (5)	-
	3	3.9 (1)	-
Female	1	3.3 ± 0.9 (10)	3.4 ± 0.5 (5)
	2	5.3 (1)	3.8 ± 0.3 (3)
	3-4	5.3 (1)	5.2 ± 0.5 (2)

Table 3. Mean (± SD) weight of *Sorex longirostris* captured at plots from which dead wood was removed (Removal) and left intact (Control). Shrews were aged using relative tooth wear. Sample sizes are given in parentheses.

		Treatment	
Sex	Age	Control	Removal
Male	1	2.8 ± 0.5 (15)	2.5 ± 0.4 (14)
	2	2.8 ± 0.4 (11)	3.0 ± 0.5 (5)
	3	3.4 ± 0.5 (10)	3.2 ± 0.5 (8)
	4	2.8 (1)	3.5 ± 0.4 (5)
Female	1	2.8 ± 0.8 (5)	2.7 ± 0.3 (14)
	2	2.6 ± 0.4 (7)	2.3 ± 0.4 (2)
	3	2.8 ± 0.6 (3)	4.0 ± 0.1 (2)
	4	3.8 ± 0.6 (3)	-

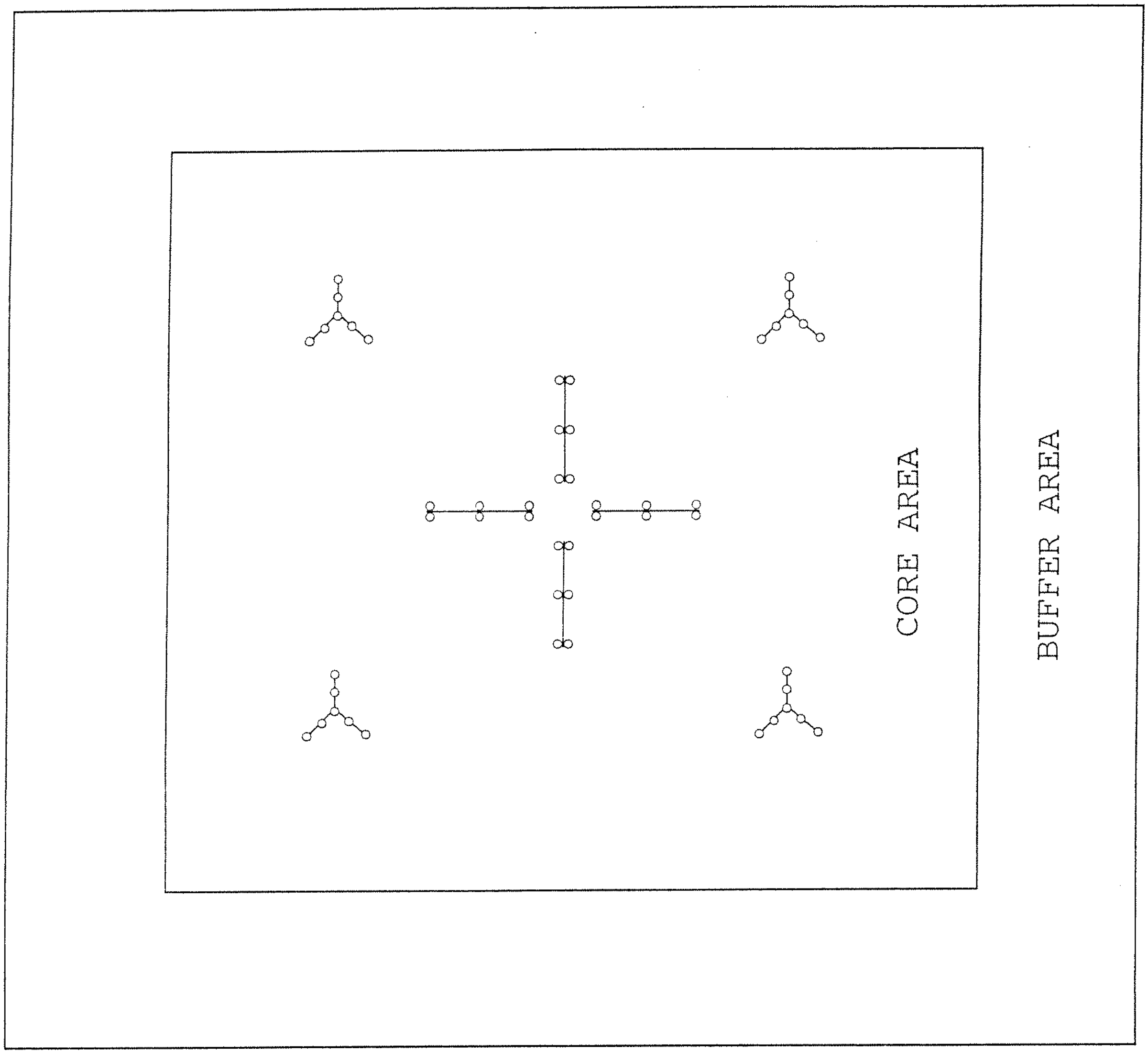

Figure 1. Layout of plots used for monitoring of shrew populations at the Savannah River National Environmental Research Park. Both core and buffer areas were subjected to experimental treatments. Lines represent drift fencing (aluminum flashing), and circles represent pitfall traps (19-l plastic buckets). Layout is not to scale.

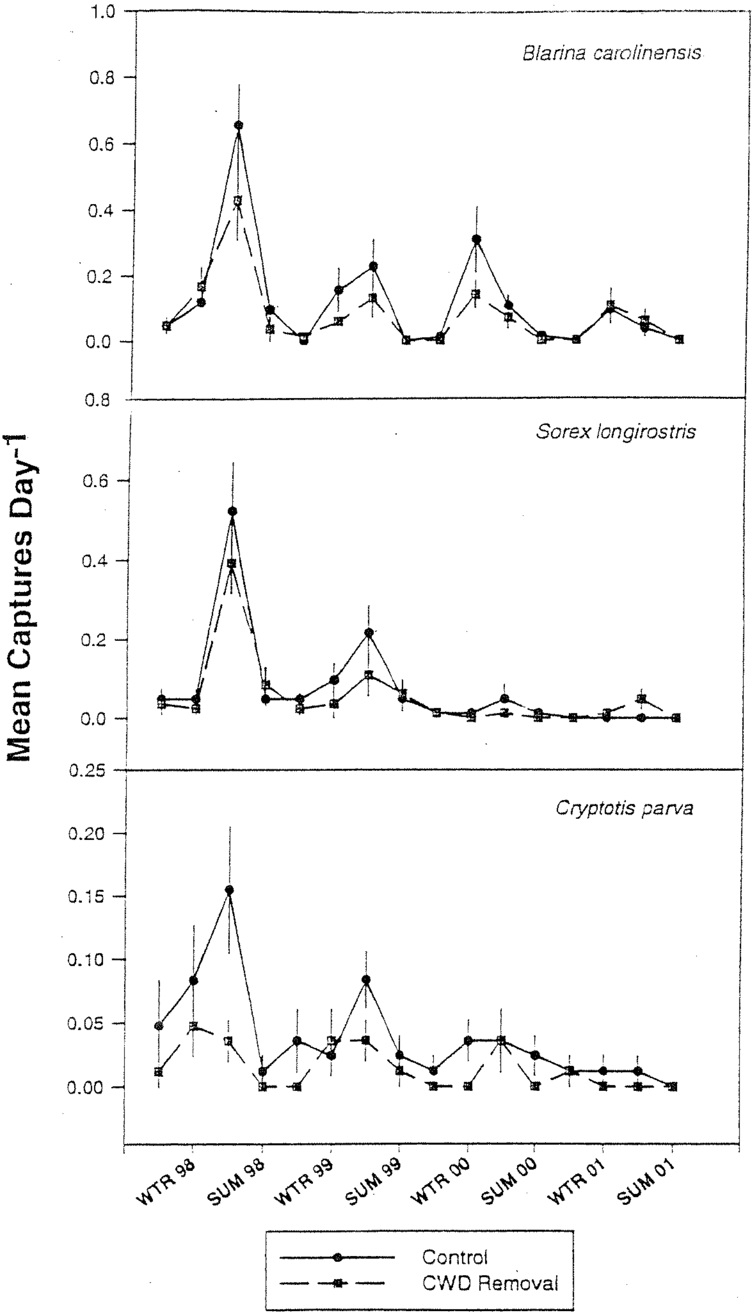

Figure 2. Capture rates of three shrews at 9.3-ha plots from which all fallen dead wood (≥ 10 cm) was removed (CWD removal; n=6) and plots from which dead wood was not removed (controls; n=6). Capture rates were mean daily shrew captures across the entire plot, including 40 pitfall traps and 350 m of aluminum drift-fencing.

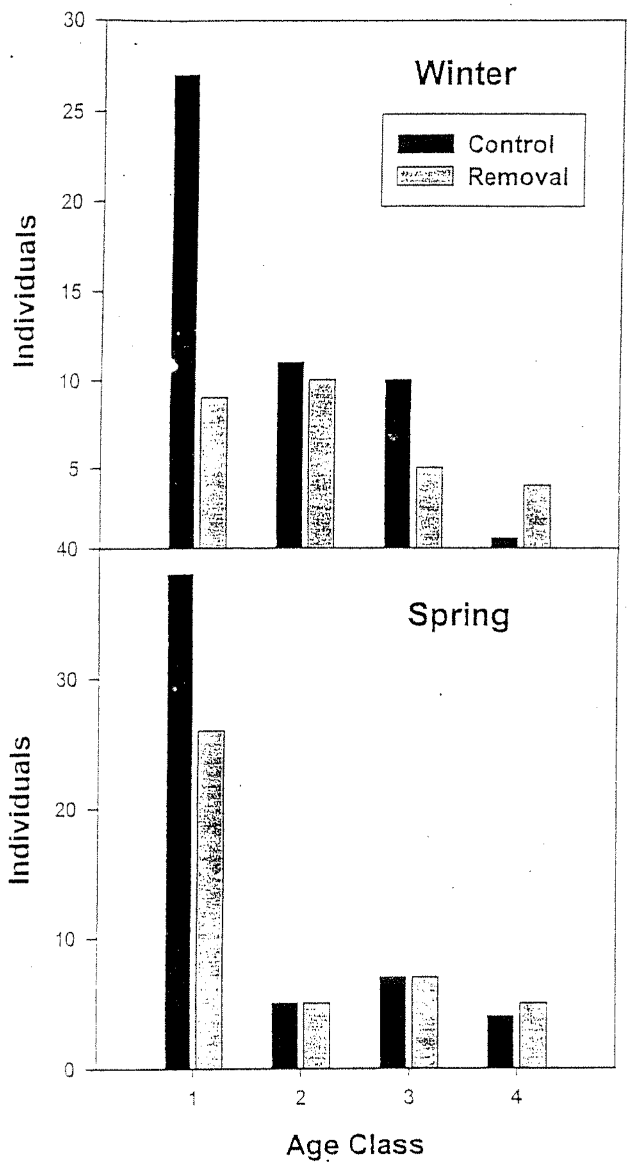

Figure 3. Age distribution of *Blarina carolinensis* captured at plots from which all fallen dead wood (≥ 10 cm) was removed and plots from which dead wood was not removed. Data were pooled across plots within a treatment. Age classification system was based on relative tooth wear following Pearson (1945).

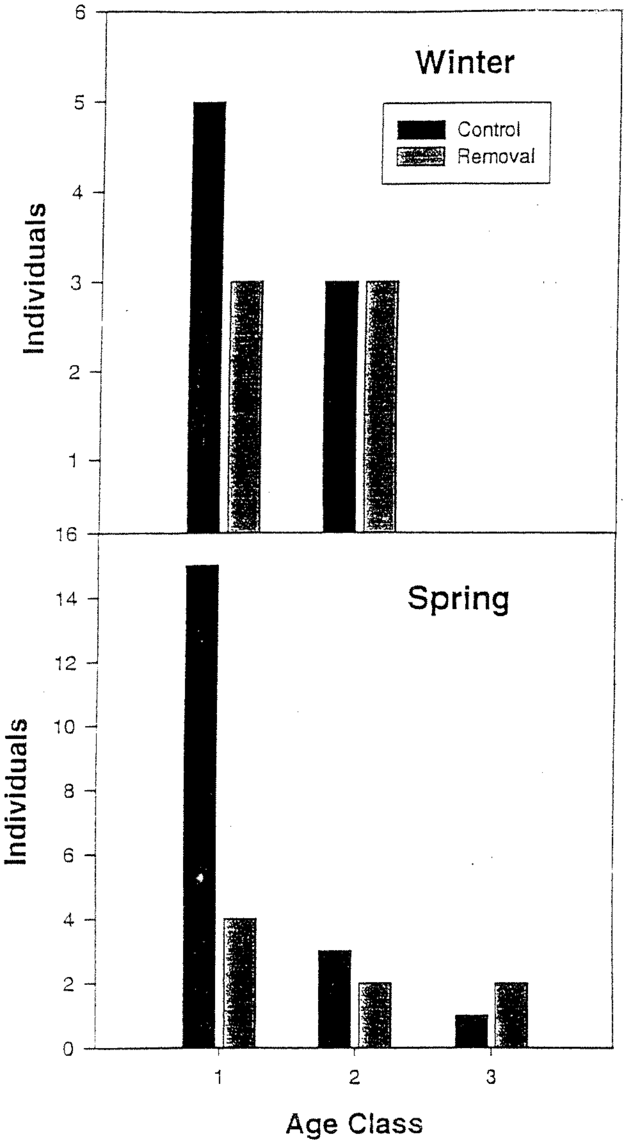

Figure 4. Age distribution of *Cryptotis parva* captured at plots from which all fallen dead wood (≥ 10 cm) was removed and plots from which dead wood was not removed. Data were pooled across plots within a treatment. Age classification system was based on relative tooth wear following Rudd (1955).

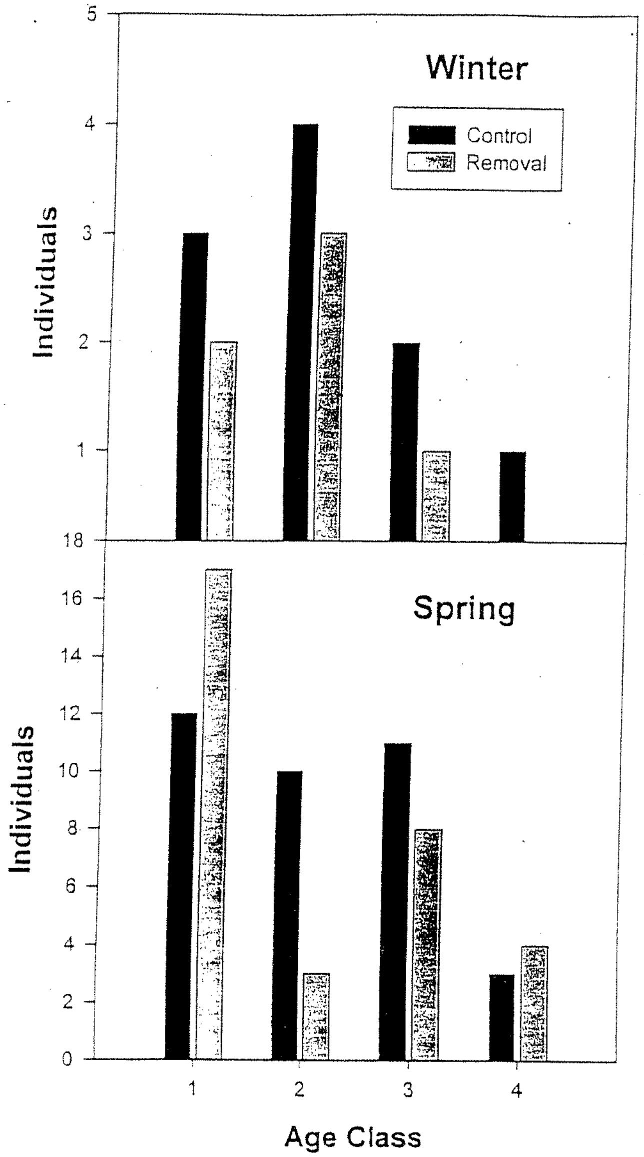

Figure 5. Age distribution of *Sorex longirostris* captured at plots from which all fallen dead wood (≥ 10 cm) was removed and plots from which dead wood was not removed. Data were pooled across plots within a treatment. Age classification system was based on relative tooth wear following Rudd (1955).

RUNNING HEAD: Herpetofaunal response to removal of dead wood

HERPETOFAUNAL RESPONSE TO LARGE-SCALE REMOVAL OF COARSE WOODY DEBRIS IN A SOUTHEASTERN PINE FOREST (PRELIMINARY DRAFT)

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Although it has been speculated that the abundance of fallen dead wood is more important to reptiles and amphibians than other vertebrate groups (Whiles and Grubaugh 1996), there exists relatively little direct evidence that dead wood influences the population dynamics of herptiles. Abundance of ensatina (*Ensatina eschscholtzii*) and clouded salamanders (*Aneides ferreus*) increased with volume of coarse woody debris (CWD) in regenerated forests of western Oregon (Butts and McComb 2000). However, MacNally et al. (2001) found no relationship between anuran or reptile abundance and CWD loads on Australian floodplains. The importance of dead wood in southeastern pine ecosystems is particularly unclear (Whiles and Grubaugh 1996).

METHODS

Data Collection.--[See preceding paper for a description of study area, treatments, and plot layout.] We sampled herptiles using a series of pitfall-drift-fence arrays and snake traps (Fig. 1). Aluminum flashing was used as drift fencing, and 19-l plastic buckets were used as pitfall traps. At each plot, we installed a single, centrally located X-shaped array (Campbell and Christman 1982) with 30-m arms. Between the central array and each corner of the plot we installed a Y-shaped array (Kirkland and Sheppard

1994) with 15-m arms. Pitfalls were kept dry and supplied with a small amount of soil and other forest debris. Two pairs of funnel traps, one on either side, were positioned along each drift-fence span in the X-shaped array. Traps were opened and monitored during a 14-day period in each of winter (January), summer (July), and autumn (October), and during a 28-day period in spring (March) between fall 1997 and summer 2001. All traps were checked daily between 0600-1200; large distances among plots and the remote nature of the study area precluded more frequent checking of traps. Herptiles were identified, weighed, and uniquely marked using toe or scale clips.

Data Analysis.—Data were analyzed using analysis-of-variance. Species were treated individually and as part of larger taxonomic groups (e.g., anurans). Seasonal samples were considered sub-samples in analyses. Thus, the sample size was 6 for each of removal and control treatment levels. We did not consider recently metamorphosed individuals (young of the year) in these analyses because dispersing young of the year are closely associated with their natal wetlands and may confound treatment comparisons (McLeod and Gates 1998). These data are treated elsewhere in this report.

RESULTS AND DISCUSSION

We captured 793 unique individuals of 6 salamander species at the study area. *Ambystoma talpoideum* was by far the most common species, with 498 captures. Capture rates of all salamanders combined did not differ between control and removal plots ($F_{1,10} = 0.99$; $P = 0.34$), nor did the capture rate of any individual species (Table 1). Three of 6 species had greater sample capture rates at control than removal plots. Of particular interest were *Plethodon glutinosus* and *Pseudotriton rubber*, because these species are non-migratory (i.e., they are terrestrial or seep breeders). So, these species might be more sensitive than other salamanders to changes in dead wood at our plots. Neither species demonstrated a negative effect of CWD removal.

We captured 563 unique anurans at the study area. Common species included *Bufo terrestris*, *Gastrophryne carolinensis*, *Pseudacris ornate*, and *Scaphiopus holbrooki*. Capture rates of all anurans combined did not differ by removal treatment ($F_{1,10} = 1.49$; $P = 0.25$). *Pseudacris crucifer* was more commonly captured at control than removal plots ($F_{1,10} = 5.00$; $P = 0.049$). Nine of 14 anuran species had greater sample capture rates at control than removal plots.

We captured 964 unique lizards at the study area in 9 species. Common species included *Anolis carolinensis* and *Sceloporus undulatus* (Table 1). Lizards as a group did not differ in capture rate between control and removal plots ($F_{1,10} = 2.55$; $P = 0.142$), nor were there any species-specific differences ($P > 0.05$). Six of 9 lizard species were captured more frequently at removal than control plots.

We captured 338 snakes in 20 different species (Table 1). Many of these species, however, were only represented by a few captures. Snakes as a group showed no significant differences between control and removal plots ($F_{1,10} = 0.20$; $P = 0.663$) nor did any individual species ($P > 0.05$). Of the 20 species of snakes captured, 14 had higher sample capture rates at control than removal plots.

In sum, we found no strong effect of CWD removal on amphibian and reptile species or higher taxa. We plan to use multivariate techniques to better understand any subtle shifts in composition occurring at these plots prior to submission of this manuscript for publication.

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Table 1. Mean capture rates (captures per 100 plot-days) at six 9.3-ha sites from which coarse woody debris (CWD) was removed and six sites from which CWD was not removed.

Taxon	Control		Removal		Sample Difference
	Mean	SD	Mean	SD	
Salamanders					
Ambystoma maculatum	0.07	0.18	0.00	0.00	–
A. opacum	0.00	0.00	0.07	0.18	+
A. talpoideum	26.56	31.78	10.57	10.16	–
A. tigrinum	0.52	0.52	0.45	0.40	–
Plethodon glutinosus	9.00	4.74	9.52	4.18	+
Pseudotriton rubber	0.07	0.18	2.23	3.80	+
All salamanders	**36.24**	**32.01**	**22.84**	**7.69**	–
Anurans					
Acris gryllus	0.30	0.46	0.30	0.23	0
Bufo terrestris	81.47	45.65	70.01	27.48	–
B. quercicus	0.00	0.00	0.15	0.23	+
Gastrophryne carolinensis	52.23	45.24	28.50	7.27	–
Hyla cinerea	0.00	0.00	0.22	0.37	+
H. femoralis	0.07	0.18	0.00	0.00	–
H. gratiosa	0.07	0.18	0.00	0.00	–

Table 1. Continued.

Taxon	Control		Removal		Sample Difference
	Mean	SD	Mean	SD	
Pseudacris crucifer	0.22	0.24	0.00	0.00	–
P. nigrita	0.15	0.36	0.07	0.18	–
P. ornate	21.88	13.19	9.23	3.55	–
Rana capito	0.00	0.00	0.07	0.18	+
R. clamitans	0.97	0.66	0.52	0.66	–
R. utricularia	1.41	1.31	1.64	1.56	+
Scaphiopus holbrooki	27.46	19.89	24.26	13.29	–
All anurans	**186.24**	**111.65**	**135.49**	**48.74**	**-**
	Lizards				
Anolis carolinensis	14.81	6.22	21.80	11.31	+
Cnemidophorus sexlineatus	0.52	0.52	0.97	1.34	+
Eumeces fasciatus	0.30	0.36	0.30	0.54	0
E. inexpectatus	1.26	0.95	0.82	0.95	–
E. laticeps	1.41	1.11	0.67	0.62	–
Ophisaurus attenuatus	0.00	0.00	0.07	0.18	+
O. ventralis	0.00	0.00	0.07	0.18	+
Scincella lateralis	4.54	3.56	8.26	6.63	+
Sceloporus undulatus	7.66	5.04	8.26	4.23	+

Table 1. Continued.

Taxon	Control		Removal		Sample Difference
	Mean	SD	Mean	SD	
All lizards	**30.51**	**11.31**	**41.22**	**12.77**	+
		Snakes			
Agkistrodon contortrix	0.22	0.37	0.00	0.00	–
Cemophora coccinea	0.82	0.52	1.12	1.12	+
Coluber constrictor	1.93	1.76	2.38	2.55	+
Diadophis punctatus	0.67	0.73	0.60	0.54	–
Elaphe guttata	0.00	0.00	0.15	0.36	+
E. obsolete	0.07	0.18	0.07	0.18	0
Heterodon platirhinos	1.04	1.00	0.82	1.18	–
H. simus	0.30	0.36	0.15	0.36	–
Lampropeltis getulus	0.07	0.18	0.00	0.00	–
L. triangulum	0.22	0.37	0.07	0.18	–
Masticophis flagellum	0.15	0.23	0.07	0.18	–
Nerodia fasciata	0.07	0.18	0.00	0.00	–
Pituophis melanoleucus	0.07	0.18	0.00	0.00	–
Sistrurus miliarius	0.15	0.36	0.07	0.18	–
Storeria dekayi	0.00	0.00	0.07	0.18	+

Table 1. Continued.

Taxon	Control		Removal		Sample
	Mean	SD	Mean	SD	Difference
S. occipitomaculata	0.82	1.07	0.67	0.62	–
Tantilla coronata	4.24	2.31	4.24	2.97	0
Thamnophis sirtalis	0.45	0.28	0.15	0.23	–
Virginia striatula	0.15	0.23	0.07	0.18	–
V. valeriae	1.86	0.82	1.12	0.73	–
All snakes	**13.32**	**4.85**	**11.83**	**6.36**	**-**

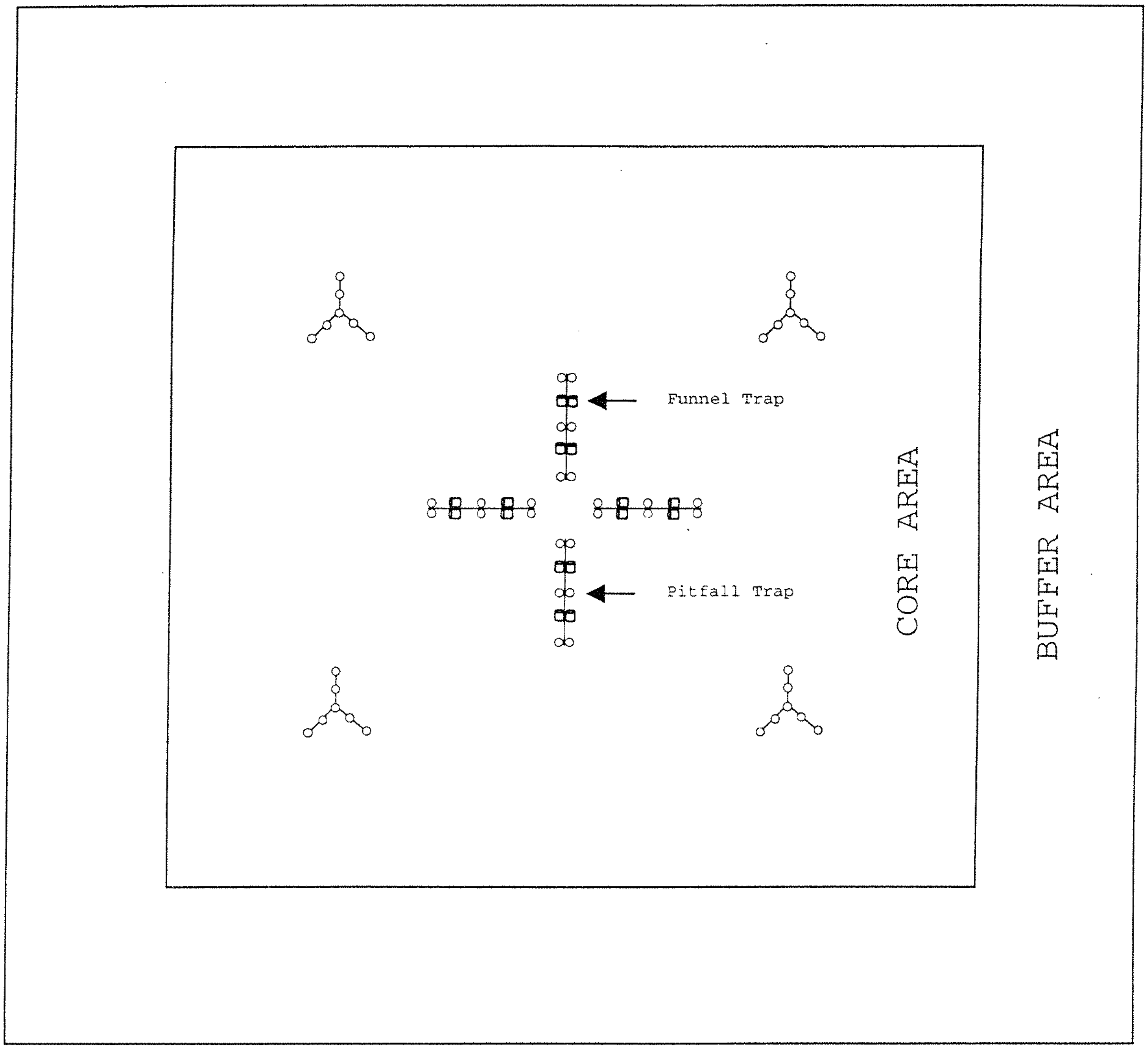

Figure 1. Layout of plots used for monitoring of herptile populations at the Savannah River National Environmental Research Park. Both core and buffer areas were subjected to experimental treatments. Lines represent drift fencing (aluminum flashing), circles represent pitfall traps (19-l plastic buckets), and cylinders represent funnel traps. Layout is not to scale.

THE WAVE OF THE FUTURE: EVIDENCE OF UPLAND DISPERSAL BY JUVENILE AMPHIBIANS, WITH IMPLICATIONS FOR LAND MANAGEMENT SURROUNDING WETLANDS

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ABSTRACT. Amphibians may serve key roles in ecosystem function, and an understanding of their biology is necessary for conserving present levels of biological diversity. However, little is known concerning the terrestrial life of semi-aquatic species. Semlitsch (1998) focused attention on maintaining the connectivity between wetlands and uplands to serve as a "life zone" for semi-aquatic amphibian species, and suggested the inclusion of a 164 m buffer zone around wetlands would be adequate to protect 95% of ambystomatid salamander populations. We present evidence that juvenile amphibians, including ambystomatid salamanders, may disperse hundreds of meters from their natal wetlands within the weeks to months following metamorphosis. Our data indicate *Ambystoma tigrinum* metamorphs can take at least six months to disperse and en route use non-polar lipid reserves garnished as larvae. Given that our data demonstrate extensive use of uplands by juvenile semi-aquatic amphibians, we suggest a land management regime following Harris (1984) that allows for both juvenile amphibian dispersal and also the consumptive use of the surrounding landscape.

Studies of amphibians suggest they may serve key roles in wetland and forest food webs and nutrient cycling dynamics (reviewed in deMaynadier and Hunter 1995; Resetarits and Fauth 1998; Fauth 1999), including the transfer of energy from wetlands to uplands. Amphibians can function as keystone predators in wetlands (Fauth 1999) and as top predators in terrestrial detrital food webs (reviewed in deMaynadier and Hunter 1995). That amphibians are implicated in nutrient and energy transfer at various ecological levels underscores their potential importance in ecosystem function. An understanding of amphibian ecology is therefore imperative for conserving present levels of biological diversity (Semlitsch 1998; Alford and Richards 1999). However, because of reported population declines worldwide, the conservation of amphibians as a group has served as a model for the study of biodiversity maintenance (Alford and Richards 1999).

Effective conservation of any animal population requires that suitable habitat is present for all life history stages of the individual members (Dodd 1996; Semlitsch 1998). A terrestrial buffer zone, or "life zone," around a wetland is required by the terrestrial phase of amphibians, and the availability of the included habitat is critical to the maintenance of the wetland's amphibian populations (Semlitsch 1998). The natural history of wetland-breeding amphibians away from breeding sites is poorly understood, however, and the distances that most species can or normally disperse are unknown (Dodd 1996; Pough et al. 1998). For semi-aquatic amphibians, information on terrestrial activity is available for few species, and is generally limited to the movement of adult animals (Dodd 1996; Semlitsch 1998). Virtually nothing is known concerning the behavior of recent metamorphic juvenile amphibians, the specific microhabitats that pond-breeding amphibians use in the terrestrial environment, or even the total terrestrial area that individuals of a species use surrounding their breeding site(s) (Dodd 1996). Recent evidence suggests that the terrestrial stage may be more important than the aquatic stage for population regulation in some species (Taylor and Scott 1997).

Conventional wisdom among herpetologists (Zug 1993; Pough et al. 2001) and data from studies of amphibian movement (reviewed in Sinsch 1990) maintain that for most semi-aquatic amphibian species, migrations to breeding sites are minimal in distance, subsequent post-breeding migrations by adults and neonates are "minor", and long-distance dispersal events are undertaken by only a small percentage of any population. Dispersal is a trait that is intrinsically linked with many aspects of population biology (Dieckmann et al. 1999), and has implications for conservation biology ranging from the determination of the minimum area needed to sustain a single population to the determination of effective reserve sizes. Based on habitat use data that are available for salamanders and other semi-aquatic species, maintaining the connection between wetlands and terrestrial habitats will be necessary to preserve remaining amphibian diversity (Semlitsch 1998).

At present, federal wetlands laws protect only habitat contained within a wetland's boundary; whereas state laws typically protect only a small (30.8 m (100 ft.)) or no terrestrial buffer zone (Semlitsch 1998). If amphibians disperse minimal distances into uplands during terrestrial movements, a 30.8 m terrestrial buffer zone may be adequate to protect enough animals to maintain population viability. Recently, several studies have addressed the amount of terrestrial habitat used by semi-aquatic vertebrates (turtles, Burke and Gibbons 1995; Buhlmann 1998; salamanders, Semlitsch 1998). Semlitsch (1998) recently challenged whether buffer zones of up to 30.8 m will adequately provide terrestrial habitat for most populations of pond-breeding ambystomatid salamanders. Data gathered from 16 studies indicated that while some individual adult salamanders move as far as 625 m from their breeding site, in most instances a buffer zone of 164 m would be adequate to protect 95% of the salamander population(s) using an ephemeral wetland.

Because some of the literature values Semlitsch (1998) used were minimum estimates and since larger buffers may be required by more vagile amphibian species, he noted that 164 m likely provided an underestimate of the area actually required by some amphibian populations.

To be effective in conservation of amphibian diversity, determinations of wetland buffer zones should be based on the biology of amphibians (Dodd 1996; Semlitsch 1998). Semlitsch's (1998) estimate for wetland buffer zones was based primarily on recorded dispersal distances of adult animals. In contrast to Semlitsch's suggested buffer zone value of 164 m to encompass 95% of a salamander population, we present evidence that juvenile amphibians use the upland landscape extensively soon after metamorphosis, confounding the problem of terrestrial buffer zone delineations that would be effective at conserving semi-aquatic amphibian species.

METHODS

Our data were collected as part of a large-scale study designed to monitor the effect of coarse woody debris on vertebrate and invertebrate diversity, conducted by the U.S.D.A. Forest Service on the Savannah River Site (SRS), near Aiken, South Carolina. Hence, the study was not designed to collect data on amphibian movement per se. Data were collected within 12 9.3-hectare study plots (Fig. 1A). The landscape contained three ephemeral wetlands, two of which (Charlie's Bay and Catastrophe Pond) were important sources of juvenile amphibian recruitment during the study period. Charlie's Bay, located to the northeast of plots 9-12, is a Carolina bay that was 10.5 hectares in size during the spring of 1998; Catastrophe Pond is a small wetland that was 0.35 hectares in size during the same period and was located centrally within study plot 1 (Fig. 1A). Apart from the wetlands noted, the next closest wetlands were approximately 1.5 km to the southwest of plot 8 and 2.0 km to the east of plots 3 and 4, respectively. The landscape included three roads (solid lines, Fig. 1A).

Amphibians were collected using drift fences constructed of aluminum flashing with 5-gallon (19 l) plastic buckets as pitfalls. Two types of fences were employed: 30 m straight fences with buckets on either side, and Y-shaped fences for which the buckets were underneath the fences and with a collecting "face" of approximately 25 m (Fig. 1B). Since an animal caught on one side of a straight fence was moving from that direction, the straight fences allowed us to determine direction of travel, whereas we could not infer direction of travel for animals collected with Y-shaped fences. The fences were arranged within each plot as shown in Fig. 1C. Distances from wetlands to fences were determined using aerial photograph imagery and ArcView 3.2 software. Fences were monitored for a 28-day sampling period in April to May, 1998, and for 14-day sampling periods in July 1998, October 1998, and January 1999. For the majority of the data, the juveniles were simply removed from the collecting buckets and released unmarked. During the winter (January) sampling period, all juveniles were marked with toe clips.

RESULTS

A total of 5,988 captures of recently metamorphosed juveniles of 13 amphibian species were made at least 200 m from the nearest likely larval site. For each of five species (*Pseudacris ornata*, *Scaphiopus holbrookii*, *Bufo terrestris*, *Ambystoma tigrinum* and *A. talpoideum*), greater than 300 captures were made that allow for the inference of dispersal patterns. Small numbers (less than 20 each) of juvenile *Gastrophyne carolinensis*, *Hyla cinerea*, *Hyla gratiosa*, *Pseudacris crucifer*, *Rana capito*, *Rana catesbeiana*, *Rana clamitans*, and *Rana utricularia* were also captured.

Pseudacris ornata. The first ornate chorus frog juveniles were collected on 16 April 1998 within plot 1 near Catastrophe Pond. By 21 April, there were seven captures, all within plot 1 (Fig. 2A). For a two-day period following a rain on 21 April, 181 captures occurred within plot 1, indicating juveniles were emerging from Catastrophe Pond. During the same period, 22 captures occurred within plot 2, at distances greater than 200 m from Catastrophe Pond (Fig. 2B). Over the following week, 651 captures occurred within plot 1, with 201 captures within plots 2 and 3, at distances of 204 m to 309 m from Catastrophe Pond (Fig. 2C). For the final week of the sampling period, a lower number of *P. ornata* captures (320) occurred within plot 1, whereas 585 captures were made at distances from 204 m to 837 m from the wetland (Fig. 2D).

Scaphiopus holbrookii. During the spring sampling period, most captures of juvenile eastern spadefoot toads were within plot 1 near Catastrophe Pond or in adjacent plots (Fig. 3A). During the summer sampling period, 337 captures of juvenile spadefoot toads were within plots 2 through 12 (Fig. 3B).

Bufo terrestris. The pattern of southern toad dispersal was similar to that of spadefoot toads. During the spring sampling period, all captures of juvenile southern toads were within plot 1 near Catastrophe Pond (Fig. 4A). During the summer sampling period, 2,897 juvenile toad captures were made across the landscape (Fig. 4B).

Ambystoma tigrinum. No eastern tiger salamander metamorphs were collected during the spring 1998 sampling period (due to a long larval period, *A. tigrinum* typically metamorphose in June or July on the SRS; D. Scott, pers. comm.). During rainless weather for the beginning of the summer 1998 sampling period, 39 captures of juvenile tiger salamanders occurred in plots 9-12 (Fig. 4A). Captures on the straight fences were in the north- and east-facing buckets, therefore Charlie's Bay, 410 m to 957 m from the capture locations, was the likely source of the animals. Following a rain on 15 July, 303 captures of metamorphic *A. tigrinum* were made on 16 and 17 July, with some at distances greater than 1 km from Charlie's Bay (Fig. 4B). No *A. tigrinum* were captured during the fall 1998 sampling period, likely due to rainless weather. When sampling resumed in January 1999, 201 captures of juvenile tiger salamanders occurred at distances from 380 m to 2,366 m from Charlie's Bay. Within 1 km of Charlie's Bay, 90% of the animals were captured in buckets facing the wetland; beyond 1 km, 93 % of the animals were captured in buckets oriented toward Charlie's Bay. Additionally, non-polar lipids (NPL) were extracted from a sample of six salamanders from each the summer 1998 and winter 1999 sampling periods, using petroleum ether in a Soxtech® apparatus. Juveniles from the winter sample had a lower NPL content per unit dry mass (χ= 8.17 % ± 2.41 S.D.) than juveniles from the summer sample (χ= 14.55 % ± 1.89 S.D., Student's one-tailed t-test, $p < 0.001$, $n = 12$).

Ambystoma talpoideum. During the winter sampling period, 1,064 unique captures of juvenile *A. talpoideum* occurred, primarily within plots 9 through 12. Our recapture rate was 6.3%. Most captures (92%) were in buckets oriented toward Charlie's Bay.

DISCUSSION

The 5,988 captures of recently metamorphosed amphibians we made at distances greater than 200 m from their likely larval sites indicates that many juvenile amphibians extensively use the upland landscape surrounding their natal wetlands. For the five most commonly captured species discussed below, our evidence indicates the majority of each population may disperse widely across the landscape soon after metamorphosis.

Pseudacris ornata. The sequence of *P. ornata* captures near Catastrophe Pond suggests that during the weeks following metamorphosis, the juveniles moved as a wave across the landscape away from the wetland (Fig. 2). Note that since our fence sizes remained the same as distance increased from Catastrophe Pond, we sampled proportionally less of the circumference around the wetland the farther the fences were from the wetland. Therefore, by the end of the sampling period, the larger numbers of captures away from Catastrophe Pond suggest the majority of the juvenile population was greater than 200 m from the wetland. An estimate of how far the population was from the wetland can be derived by weighting fence distances from the wetland with the number of metamorphs caught per fence. Considering plots 2, 3, 6, and 7 to be where the majority of juveniles were at the end of the sampling period, the main wave of dispersing animals was at least 306 m from the wetland within 2 weeks following metamorphosis. Captures within plots 4, 5, and 8 during the final week of sampling indicate the leading edge of the wave was approximately 683 m from Catastrophe Pond.

Scaphiopus holbrookii. The 337 captures within plots 2 through 12 during the summer 1998 sampling period indicate that juvenile *S. holbrookii* also travel hundreds of meters from their respective natal wetlands within several months following metamorphosis (Fig. 3B). The fact that four metamorphs were captured in plot 10 during the spring sampling suggests the one-hectare wetland to the southwest of Charlie's Bay may have been a site of spadefoot toad recruitment (Fig. 3A). Since several larval sites likely were involved, the data do not appear as a single wave moving across the landscape. However, since larger numbers of animals were captured in plots 2 through 4 as compared to plot 1 during the summer sampling (Fig. 3B), the data indicate the majority of juvenile spadefoot toads dispersed beyond 200 m from Catastrophe Pond.

Bufo terrestris. The 2,897 captures of southern toad juveniles during the summer sampling period also indicate long distance dispersal from multiple larval sites (Fig. 4B). The 491 captures in plot 8 were likely animals that had dispersed from a wetland 1.5 km to the southwest, whereas the 948 captures in plots 3 and 4 likely represented animals that had dispersed from wetlands 2 km to the east of those plots.

Ambystoma tigrinum. The sequence of juvenile *A. tigrinum* captures also suggests the animals disperse as a wave across the landscape (Fig. 5). During the January sampling, 90% to 93% of the *A. tigrinum* captures were in buckets indicating movement away from Charlie's Bay, suggesting dispersal continued for at least 6 months following metamorphosis (Fig. 5C). That individuals from the winter sample had lower NPL levels than individuals from the summer sample indicates juvenile tiger salamanders use energy reserves obtained as larvae in wetlands to disperse long distances over land as recent metamorphs. Since as many individuals were captured at distant fences as compared to fences nearer to Charlie's Bay during the winter sampling period (Fig. 5C), more individuals may have been at distances $\geq$ 1 km from the wetland as compared to $\leq$ 1 km from the wetland.

Ambystoma talpoideum. The majority of the 1064 captures were in plots

9 through 12, 380 m to 1005 m from Charlie's Bay. That 92% of the captures occurred in buckets oriented toward Charlie's Bay indicate that *A. talpoideum* metamorphs also were moving as a wave away from the wetland.

Several factors may contribute to the lower numbers of captures for the remaining eight species. Any given species may simply be rare at the study site (e.g., *Rana capito*). The fences may not have been monitored during the dispersal "window" for some species (e.g., late May/early June for *Rana utricularia*), and some species, such as hylids, were likely effective at escaping the pitfalls. Finally, it is possible that juveniles for some species may have remained close to their natal wetland.

Evidence indicating juvenile anurans disperse widely soon after metamorphosis has been reported previously. Dole (1971) presented data that juvenile *Rana pipiens* commonly traveled up to 800 m within 2 to 3 days following metamorphosis, and described this dispersal as "large waves" entering a study site from a remote wetland. Freeland and Martin (1985) found the expansion of *Bufo marinus* in Queensland, Austrailia occurred mainly due to the continual colonization of new areas by small, sexually immature toads. Breden (1987) showed that juvenile *Bufo woodhousei fowleri* were more vagile than adults. Note that two of our five common species were ambystomatid salamanders, belonging to the group in Semlitsch's (1998) analysis. Therefore, even species that are relatively sedentary as adults may be more vagile as juveniles.

The demonstration that juvenile amphibians extensively use uplands has important implications for amphibian conservation. As noted by Semlitsch (1998), the exclusion of adequate upland area from protection would most likely reduce recruitment of juveniles into the adult breeding population. However, creating a buffer zone up to 164 m from a wetland's edge (Semlitsch 1998) may be inconsequential for amphibian populations if as juveniles the majority travel several hundred meters farther from the wetland. By the same token, protecting land for hundreds of meters around small, temporary wetlands may not be practical in most cases. Furthermore, legislation to mandate protection for extensive tracts surrounding wetlands is unlikely, and a request to foresters and land managers to preserve such large areas will not likely be met with much enthusiasm. This may be particularly true for wetlands that do not fill each year and for which failure in amphibian recruitment is the norm, regardless of the wetland's importance for recruitment during "wet" years.

We suggest two options for land management to allow for dispersal of juvenile amphibians. The first, where feasible, is to allow the wetland(s) to remain embedded in large expanses of intact forest or other natural landscape. Such a strategy would not only favor local population persistence, it may also permit the maintenance of metapopulation dynamics (Marsh and Trenham 2001). Of course, such an option will not likely be possible in most cases. For managed land surrounding such wetlands, we therefore suggest a management scheme similar to that proposed by Harris (1984) for timber management surrounding an old growth stand. In this case, the land surrounding the wetland is divided into wedges (compartments) radiating from the wetland, with timber cuttings (or other consumptive management practices) beginning in Compartment 1 and following in sequence through a cycle (Fig. 6). Time between loggings or other uses (e.g., agriculture) will depend on forest or natural habitat type, time to forest maturity or habitat recovery, etc. For our example, we suppose a southeastern U.S. pine forest with alternate compartments logged at 10-year intervals (Fig. 6). Such a management scheme ensures that mature forest or other relatively "natural" habitat is available for juvenile amphibian dispersal at all periods through the management sequence, thereby promoting amphibian diversity while allowing land managers to use large areas surrounding wetlands for production. Evidence from wood frogs (*Rana* *sylvatica*) and spotted salamanders (*Ambystoma maculatum*) indicates that juvenile amphibians may preferentially disperse through closed canopy forest as compared to recent clearcuts (deMaynadier and Hunter 1999), favoring the suggested management regime. Whether the proposed scheme would be appropriate for other semi-aquatic organisms is unknown.

In conclusion, we agree with Burke and Gibbons (1995) and Semlitsch (1998) that maintaining connectivity between wetlands and uplands will be necessary to effectively manage for populations of semi-aquatic species. However, in light of our data, we do not think biologically-meaningful terrestrial buffer zones can realistically be mandated. We therefore suggest that land managers employ management schemes which allow for productivity from the landscape while minimizing deleterious effects to populations of semi-aquatic organisms.

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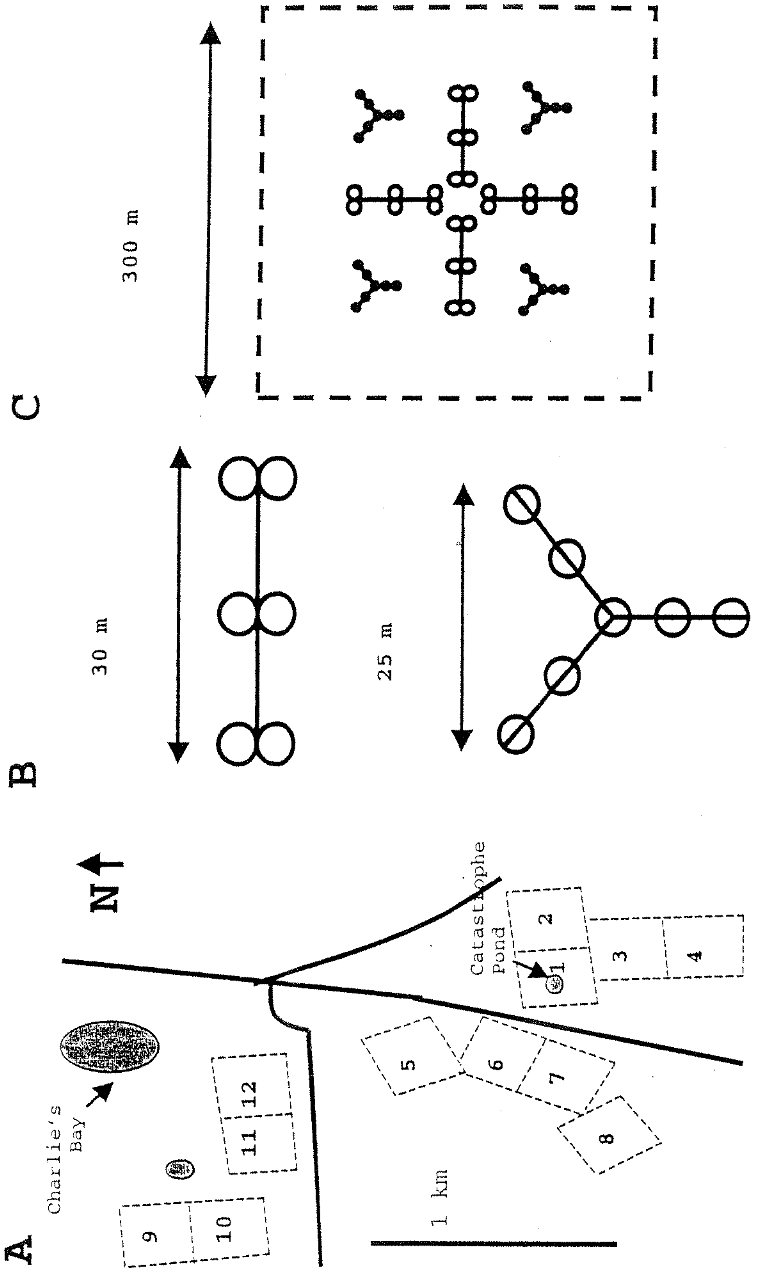


Fig. 1. A. Arrangement of study plots (dashed areas) and wetlands (shaded ovals) on landscape. Solid lines indicate roads. B. Illustration of two types of drift fences used during the study. C. Arrangement of drift fences within each study plot.

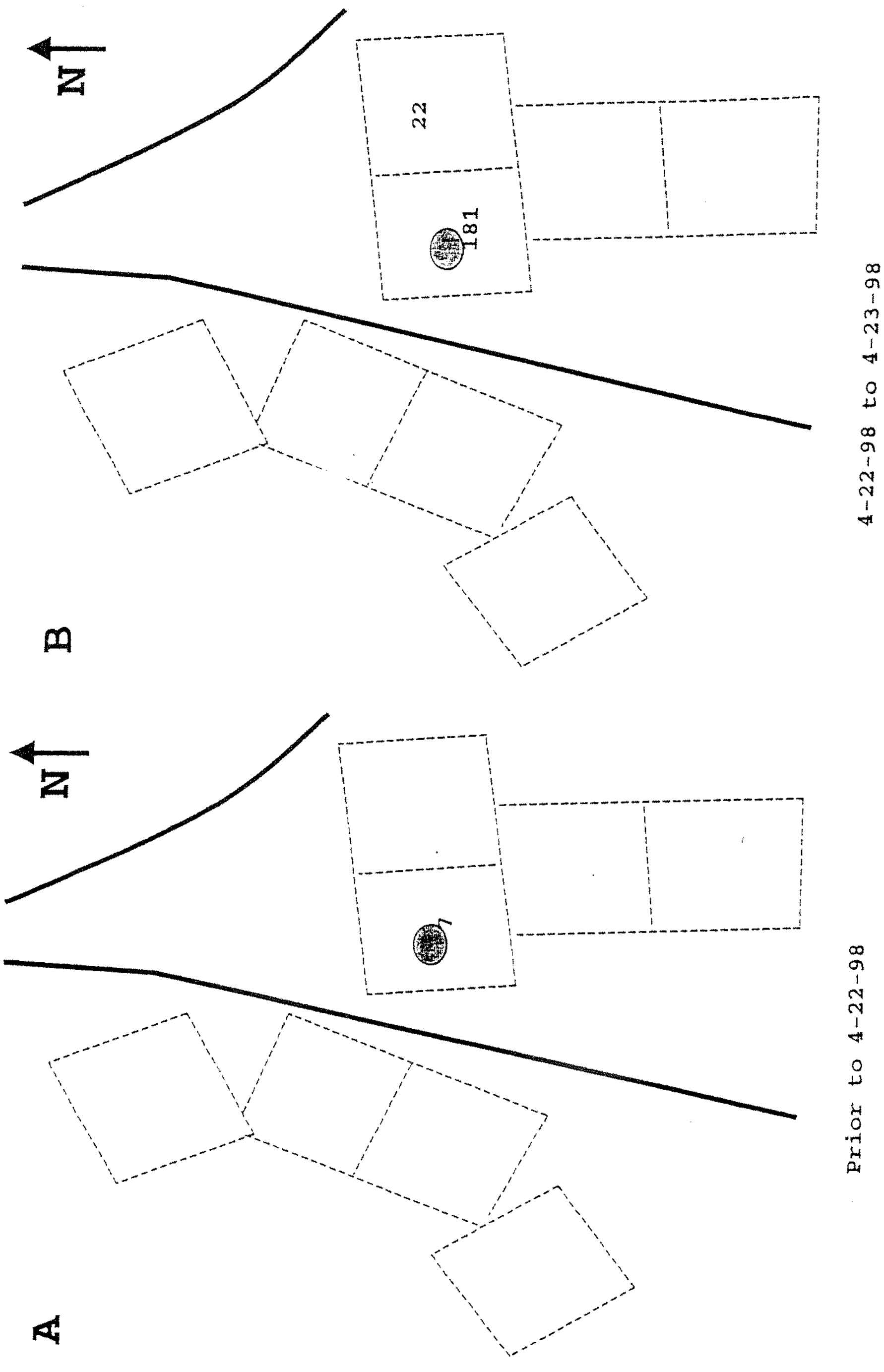
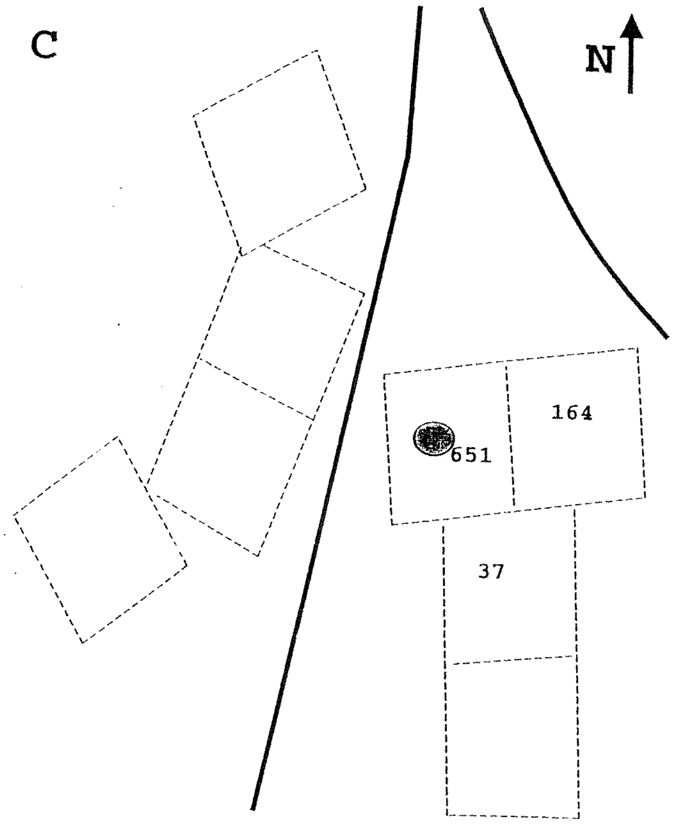


Fig. 2. Sequence of captures for *Pseudacris ornata* juveniles during the spring sampling period. A. Captures prior to 4-21-98. B. Captures on 4-22-98 and 4-23-98. C. Captures from 4-24-98 to 5-1-98. D. Captures from 5-2-98 to 5-9-98.

C



4-24-98 to 5-1-98

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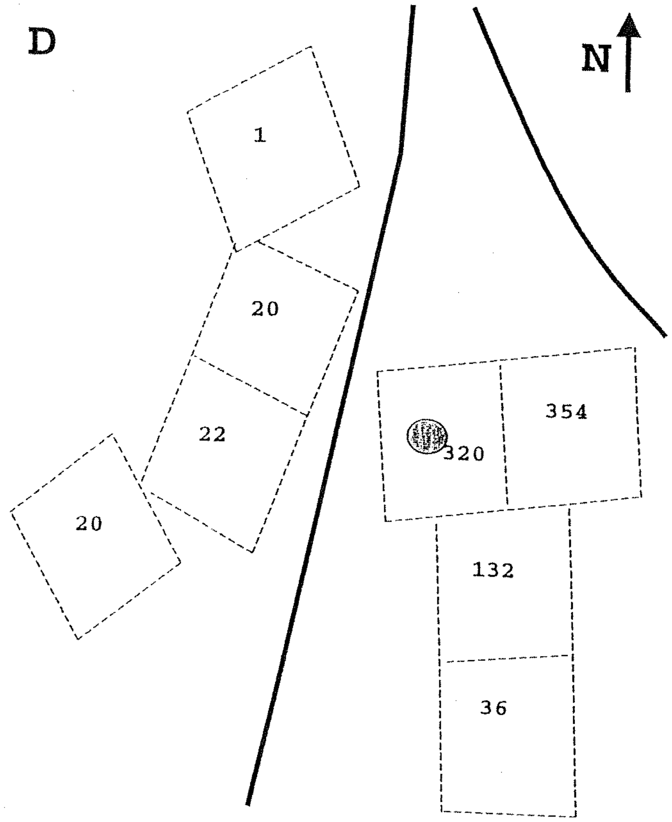

5-2-98 to 5-9-98

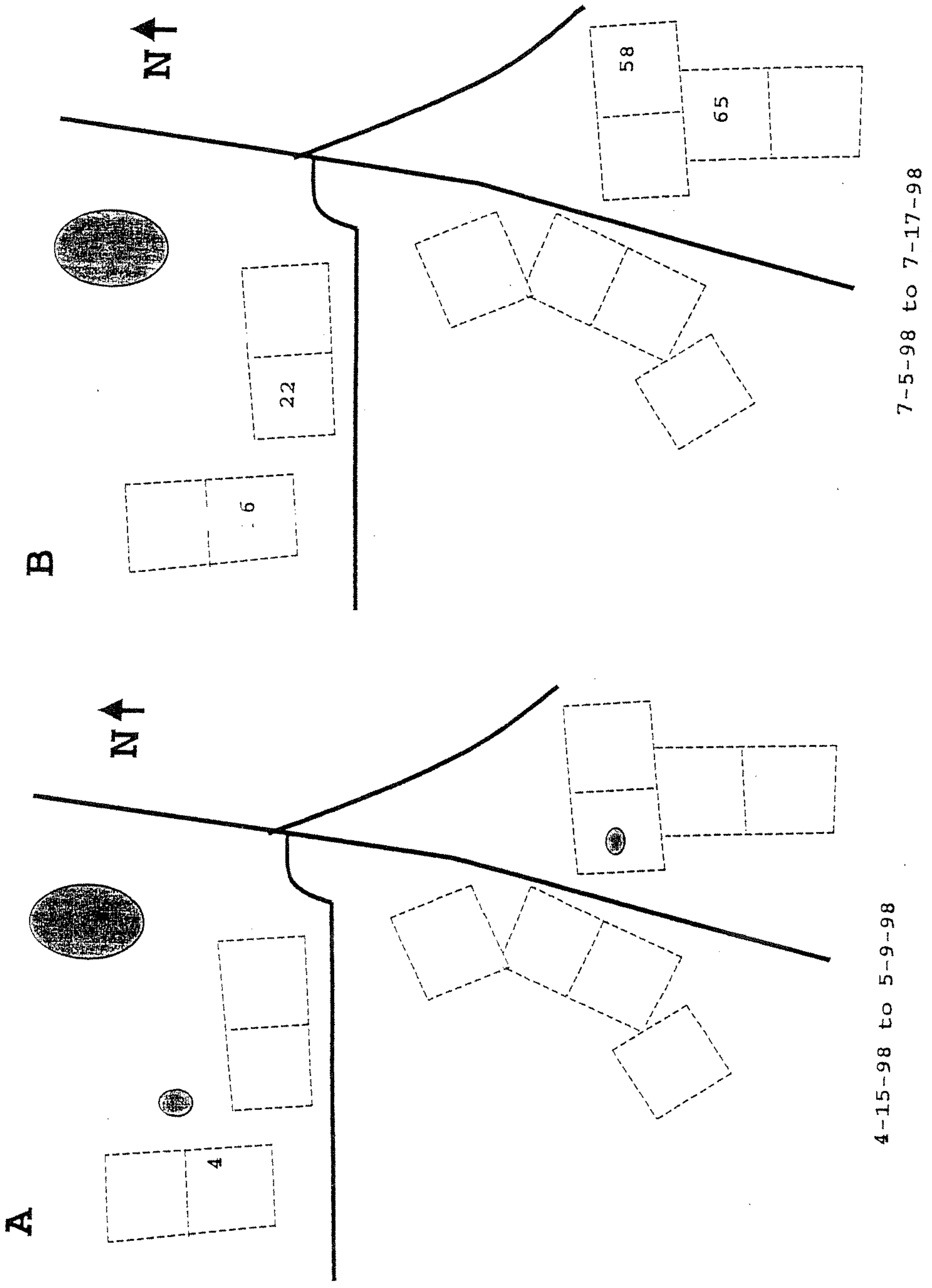

Fig. 3. Sequence of captures for *Scaphiopus holbrookii* juveniles. A. Captures from 4-15-98 to 5-9-98. B. Captures from 7-5-98 to 7-17-98.

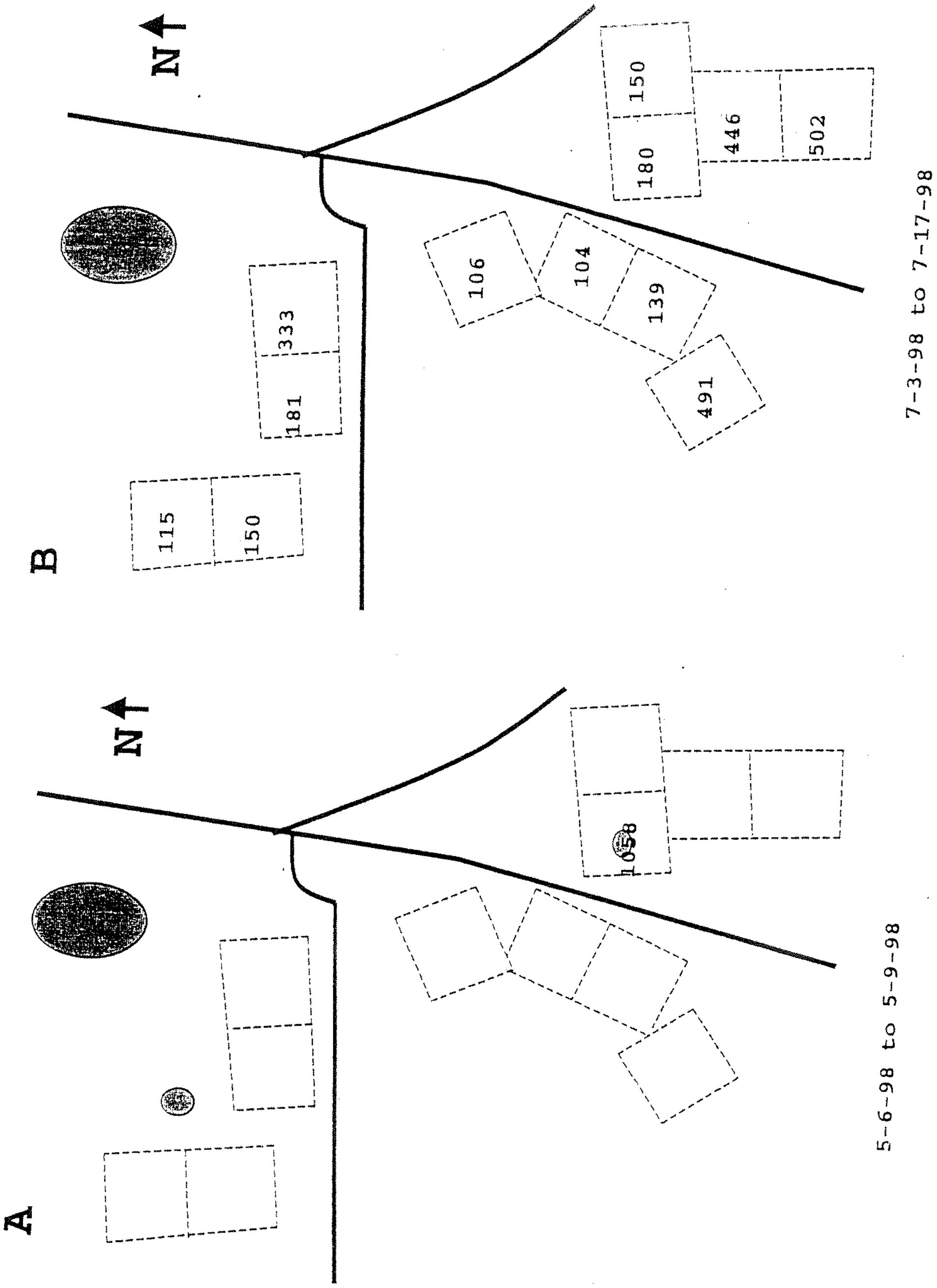

Fig. 4. Sequence of captures for *Bufo terrestris* juveniles. A. Captures from 5-6-98 to 5-9-98. B. Captures from 7-3-98 to 7-17-98.

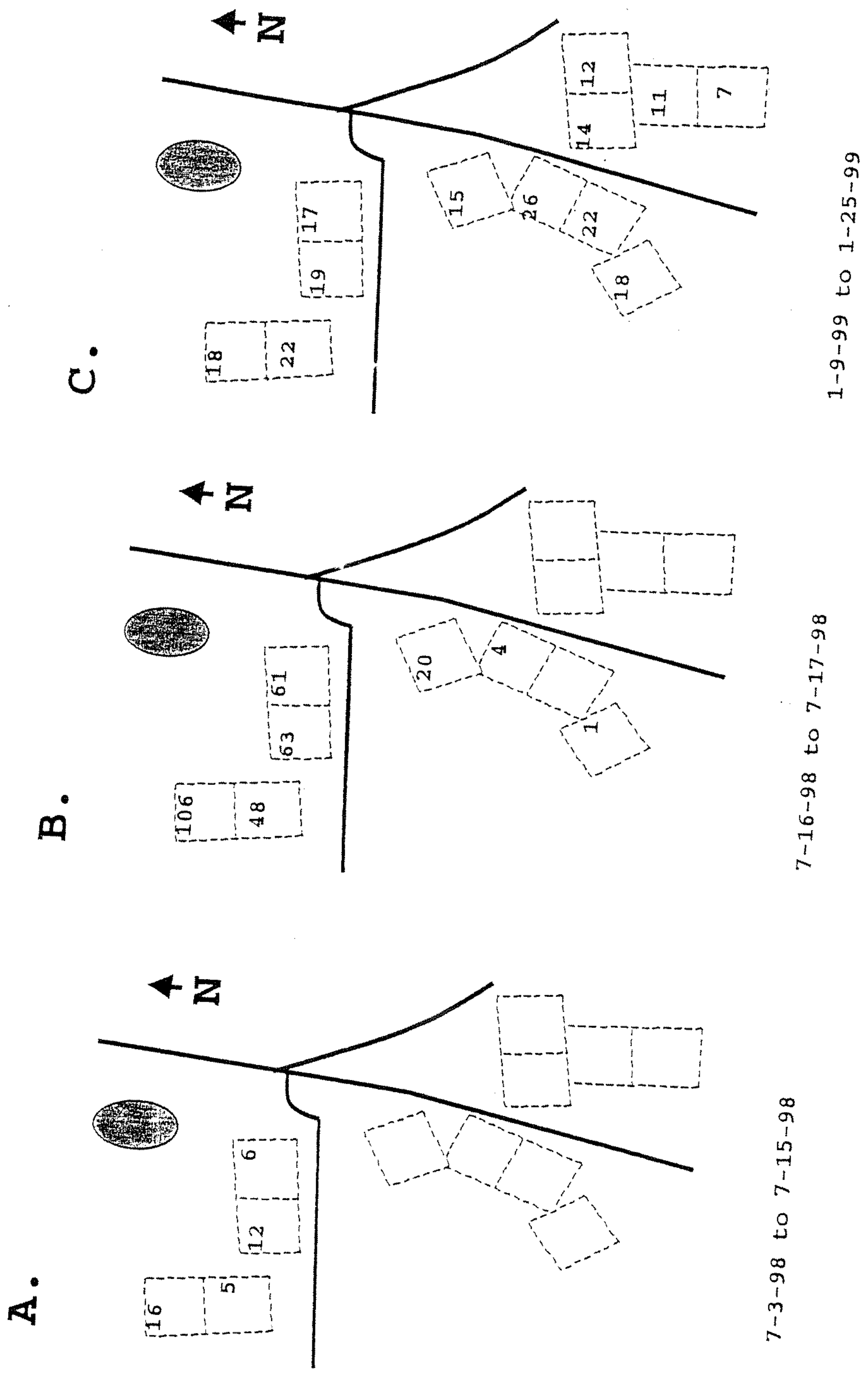

Fig. 5. Sequence of captures for *Ambystoma tigrinum* juveniles. A. Captures from 7-3-98 to 7-15-98. B. Captures from 7-16-98 to 7-17-98. C. Captures from 1-9-99 to 1-25-99.

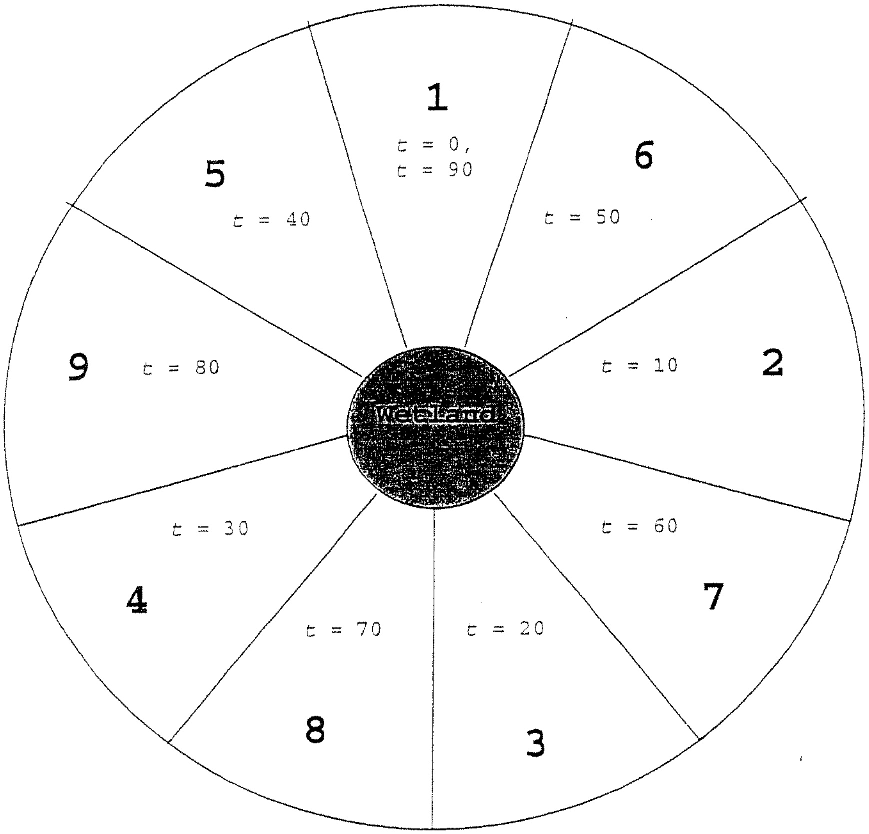

Fig. 6. Suggested sequence of land use surrounding a wetland, after Harris (1984). In this example, alternate compartments of pine forest are logged at 10 year intervals.